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A layered defense against plant pathogens

Microbial consortia may be key to robust protection of roots from disease

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Diseases affecting crops take a toll on agricultural yields worldwide. Strategies to eradicate or mitigate these pathogens include breeding resistant genotypes, crop rotation, and chemical or biological treatments. A phenomenon called "suppressive soils" has attracted considerable interest because such soils can reduce disease incidence despite pathogen presence, a susceptible host and favorable conditions for infection. If the secrets of suppressive soils could be unlocked, it might be possible to confer suppressiveness to other soils without the risks and losses associated with repeated cropping on disease-affected fields. Suppressive soils have long been suspected to be mediated by microbiota, particularly because suppressiveness is lost upon sterilization and can be transferred from one soil to another through mixing. On page XXX of this issue, Carrión *et al.* (*1*) demonstrated that they could confer disease suppressiveness when specific bacteria were added as a consortium to a conducive soil.

Suppressive soils can exhibit both general suppression, in which disease incidence of a range of pathogens is reduced, or specific suppression, in which a particular pathogen's impact is dampened. These have been compared to innate and adaptive immune responses, respectively (*2*). General suppression is typically attributed to competitive exclusion of pathogens by an active microbiota and appears inherent to the soil. Specific suppression typically arises after multiple seasons of growing a susceptible crop in the presence of a pathogen, during which an initial high disease incidence drops with each successive growth season. This suppressive activity remains as long as the susceptible crop is grown in the soil, but can quickly dissipate if another crop is grown or new pathogens are introduced. However, which soils are likely to develop suppressive activity in subsequent growth seasons after a disease outbreak is unknown and challenging to test.

Careful microbiological work has identified a handful of microorganisms that contribute to suppression of specific pathogens (*3, 4*). Over the past decade, molecular methods have accelerated these studies and started to reveal a complex interplay of organisms, genes and biochemical factors that contributes to this intriguing process. Carrión *et al.* identified and cultivated several bacteria whose abundance inside plant roots was increased upon inoculation of a plant with the fungal pathogen *Rhizoctonia solani* in suppressive soil. Notably, the ability of these organisms to penetrate into the plant roots indicates their interactions with the plant host may be equally critical to suppression as direct interactions with the pathogen. Moreover, the increased effectiveness of the consortium compared to individual isolates implies they may interact with each other as well (see the figure).

The investigators also identified key bacterial genes that increased in expression upon plant infection in suppressive soil – hinting at the mechanisms of pathogen suppression and pointing toward the development of robust consortia that confer the suppressive phenotype. These genes include carbohydrate-degrading enzymes, especially those potentially active against fungal cell walls, and biosynthetic gene clusters (BGCs) for specialized metabolite production. Most notably, one of the BGCs in the disease-suppressing *Flavobacterium* isolate was demonstrated to be critical for full disease suppression through site-directed mutagenesis.

The Carrión *et al.* study focuses on *Rhizoctonia*, a genus of fungi encompassing pathogens of diverse crops that cause considerable global yield losses, including the causative agents of bare patch and root rot of wheat, rice sheath blight, and root and crown rot of sugar beet. Soils suppressive to *Rhizoctonia* pathogens have been observed in various fields across the globe, including the Dutch site examined by Carrión *et al*. Previous work from this group has demonstrated that certain species of *Paraburkholderia*, *Pseudomonas* and *Streptomyces* are increased in abundance near roots (rhizosphere) of plants grown in these *R. solani* suppressive soils, and that some isolates of these genera can confer suppressive activity (*5, 6*). This activity has been linked to production of a chlorinated lipopeptide (thanamycin) by *Pseudomonas* and of sulfurous volatile compounds by *Paraburkholderia* (see the figure). As suggested by Carrión *et al.*, these rhizosphere inhabitants may form the first line of defense against soilborne *Rhizoctonia*; subsequent attack and colonization of plant roots by the pathogen prompts the plant to mobilize a second line of defense by bacteria inside the root. Not all isolates with disease-suppressive activity *in planta* also exhibit antifungal activity *in vitro*, implying additional signals or factors are required for disease suppression (*6*).

Studies of *R. solani*-suppressive soils at other locations have identified other bacterial strains and genes involved in suppression, implying there are many paths to success and therefore many promising avenues to pursue in developing agricultural products or practices to build suppressive activity (*4*). The bacterial strains and consortia tested by Carrión *et al.* have only been demonstrated to confer suppressive activity on nearby conducive soils with similar biogeochemistry and microbiology. Individual microbes often fail to establish and confer disease suppression when seeded into new environments; it is hoped that synthetic consortia will prove more successful at displacing indigenous microbiota in addition to working synergistically to inhibit pathogens (*2*), but evidence for this is anecdotal so far. Moreover, there may be additional physical, chemical and microbiological features that enable suppression at particular locations and not others that have yet to be characterized.

Demonstrating disease suppression by a microbial isolate or consortium in a variety of conducive soils, particularly in a field setting, would be a major advance. If, as seems likely, suppressive activity is dependent on the soil background, controlled experiments on sterile growth substrates could help eliminate the “unknowns” associated with growth in soil, including the presence of other pathogenic or beneficial microbes (*7*). Inoculation into sterilized soils that have lost suppressive activity, particularly cross-inoculations with other suppressive soils, could also help distinguish physical and chemical factors from biological, establishing, for example, requirements for specific nutrient levels for suppression to be effective. Ultimately, such studies could build a “recipe” for reliable disease suppression that is robust to field variability.

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Plant-pathogen-microbiota interactions

The plant, the endophytic microbiota and the rhizosphere microbiota defend the plant against pathogen attack. However, there is more to be learned about how these defenses are coordinated (dotted arrows).